THE VESSEL IN SEED PLANTS[1]

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(WITH PLATES XVI–XX)

In view of the recent discussion of the evolution of the vessel in Gnetales and Angiosperms by THOMPSON (5), it was suggested to the writer that a comparative study of the vessel in seed plants would be of interest in bringing forward more evidence which might have weight for or against the theory that the presence of vessels in these two groups is an argument for genetic relationship. The discussion of scalariform pitting in the secondary wood of Angiosperms by BROWN (2) also suggested the larger question of the origin of the vessel in seed plants, that is, has it been derived from the pitted tracheids of the more primitive plants, or is the scalariform vessel the more primitive, from which the pitted vessel has been derived?

By way of introduction I wish to discuss briefly the vessel of *Pteris aquilina* as an example of the lower vascular plants. The side wall, usually at a definite angle with the end wall, is marked with scalariform bordered pits (fig. 1, right). The borders are very clearly evident in the profile view of the vessel (fig. 4). The typical end wall of the vessel is characterized by scalariform perforations in which the border has wholly disappeared at the center, but is still visible at both ends of the perforation (fig. 3). The difference between the openings in the side and end walls is again very clearly seen in the profile view of the vessel (fig. 4). The border has practically disappeared from the perforation, although occasionally it is evident near the juncture of the end wall with the side wall. Another striking difference in the perforations of side and end walls is the reaction to stains. The end wall gives a definite cellulose reaction with haematoxylin, while in the side wall blue is present only in the middle lamella and the pit membrane, the border of the perforation taking a definite lignin stain with

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safranin. This difference separates very distinctly the side and end walls when viewed under the microscope. An interesting condition is seen in fig. 1, where the end wall at the center is perforated by a series of bordered pits which gradually grade into scalariform pits and perforations at the lower end of the figure. Fig. 2 shows an end wall which is clearly reticulated, a stage intermediate between the typical scalariform perforation and the more unusual pitted type. It is interesting to note in this connection that in the higher groups of the Filicales (Osmundaceae and Ophioglossaceae) the side wall of the vessel is likewise pitted and not scalariform as in most ferns. These observations as seen in figs. 1 and 2 give weight to the view that the end wall is the more specialized portion of the vessel and more advanced in its organization, and that in the pitted end wall of *Pteris* we have the forerunner of the pitted type of perforation characteristic of the lateral walls of the element in the higher groups.

Gnetales

Turning now to the vessels of the seed plants, we may consider first the vessels of Gnetales. The vessels in the young twig of *Ephedra* (fig. 5) show perforations which are clearly bordered pits. Although the torus has entirely disappeared and the border is very much reduced in nearly all of the pits, the torus is present in two of the pits in the upper portion of the vessel at the right. Fig. 6 shows larger vessels of an older twig, the vessel at the right being more advanced than the vessel at the left. Here the perforation consists of a series of bordered pits in which the membrane has entirely disappeared. Since the end wall of the vessel is the most specialized, it would naturally show the greatest advance in development, and this is true in the higher types of Gnetales. In radial sections of the stem of the *Gnetum Gnemon* type (figs. 7, 8) all stages are found, from the clustered bordered pits of the *Ephedra* type to the open pore of the higher forms, and transitional fusion perforations are clearly seen (fig. 7). The mature stem of the *Gnetum Gnemon* type is illustrated in fig. 9, where the vessels are characterized by the typical porous perforations of the higher forms. In contrast with the *Gnetum Gnemon* type, *Gnetum scandens*, an advanced vine species of the genus, is interesting.

While the vessels of this type in the mature secondary wood of the stem are also characterized by the large bordered open pores, a consideration of the primitive regions, such as the primary wood and the wood of the leaf trace, shows that the open pore has been derived from pit fusions. Fig. 10 illustrates a radial section of the stem of *Gnetum scandens* cut directly through the primary wood. A protoxylem element with its spiral markings is visible just at the left of the vessel. At the lower part of the figure the pits are quite distinct, suggesting the *Ephedra* type, but in the center the fusion is practically complete. In the leaf trace of *Gnetum scandens* (figs. 11, 13) is a condition similar to the perforation found in the older twig of *Ephedra*, showing the scalariform pits obviously the result of the fusion of bordered pits. A higher magnification of a similar perforation is shown in fig. 12, bringing out more clearly the borders of the pits. Thus in *Gnetum scandens* we do not find always the fusion of pits haphazardly arranged as THOMPSON (5) describes for *Gnetum*, but fusion of pits side by side (figs. 12, 13), a condition which, as shown later, is paralleled in the fusion of pits in the vessels of Angiosperms.

Welwitschia shows the open bordered pore type of perforation in the vessel of the mature wood (fig. 14). The border of the pit is clearly visible in the vessel to the left, while in the vessel to the right the edge of the perforation faces the observer. The vessel of the leaf trace in *Welwitschia* (fig. 15) shows the more primitive type of vessel as found in *Ephedra*. Thus the monotypic genus *Welwitschia* illustrates the same general principles shown for *Gnetum*, namely, that in the vessel wall of primitive regions is found the *Ephedra*-like type of vessel with pitted perforation. It may be added that *Welwitschia* and *Gnetum* are usually distinguished from *Ephedra* by absence of the torus in the bordered pit.

Angiosperms

Liriodendron and *Magnolia* may be considered as representatives of a possibly primitive group of Angiosperms, the Magnoliaceae. In the side wall of the vessel is the same general principle illustrated in the end wall of the Gnetales. Fig. 16 shows vessels in the mature secondary wood of a small twig of *Liriodendron Tulipifera*. Here the vessels, both the lateral wall and the perforations, are obviously scalariform. This situation has recently been emphasized by BROWN (2) as showing the derivation of the vessel of Angiosperms from the scalariform tracheid. The condition found in the primitive regions of *Liriodendron*, however, particularly the primary wood of the root, by no means seems to justify this conclusion. Fig. 17 shows a radial section in the region of the primary wood of the root of *Liriodendron Tulipifera*. All three vessels are characterized by pitted lateral walls and not by scalariform sculpture. A higher magnification of a portion of the vessel seen at the extreme right is shown in fig. 18. The center of the vessel exhibits scalariform perforations. It is equally clear that this scalariform perforation passes gradually into pits both above and below. Fig. 19 shows the perforation above and the lateral wall of the vessel below, with the gradual transitions from pits to perforations particularly clear. The perforations show the so-called "ghosts" of former pits, which become more and more pitlike as one passes downward, until the typical bordered pits become clearly recognizable. Still another illustration of the same phenomenon is seen in fig. 20. It is clear from these illustrations that in *Liriodendron Tulipifera* there is a gradual transition from pits to scalariform perforations in the vessels of the primary wood.

It is evident that the perforations of the vessels in Filicales and Gnetales represent the most advanced condition of the vessel wall. The obvious interpretation, as seen in *Liriodendron*, is that the side wall represents the primitive pitted condition, while the perforation has been derived from the fusion of pits precisely as in *Gnetum* and *Welwitschia*. The seriation of events cannot possibly be regarded as reversible, for if that were the case, we should have to regard the perforation as representing the primitive condition of the vessel wall, a position which is untenable.

Magnolia Frazeri has a greater tendency to scalariform perforations and lateral pitting than the other species of the genus which have been observed. As in *Liriodendron*, the most interesting condition here is found in the region of the primary wood of the root. Fig. 21 shows a radial section through this region. The perforation in the center gradually grades into pits above and below, a condition practically identical with a similar section of the root of *Liriodendron* as seen in fig. 18. Fig. 22 illustrates the character of the vessel in the first annual ring of a branch of *Magnolia Frazeri.* The perforation is obviously scalariform, while the lateral wall is characterized by typical pits. The end wall perforations again show evidence of fusion of pits in the "ghosts" and indentations on the scalariform openings. In many instances scalariform perforations may be seen to grade into pits in the wood of the stem of *Magnolia Frazeri.* It seems clear from a study of the primary wood region of the root of *Liriodendron* and *Magnolia* that the vessel with pitted walls is antecedent to the vessel with scalariform walls, and further that the scalariform perforations which are universal in the vessels of *Liriodendron Tulipifera* and are likewise found frequently in the vessels of species of *Magnolia* are the result of fusions of pits precisely as in the case of the perforations of the vessels of *Gnetum* and *Welwitschia* in Gnetales. Since evidence from primitive regions in Gnetales has been used by THOMPSON (6) in tracing the origin of the perforations in vessels of that group, the validity of a similar procedure as regards the evidence in the Magnoliaceae obviously must be admitted.

As another representative of the Ranales, the ranunculaceous genus *Paeonia* is interesting as showing in the vessels of the stem typical scalariform perforations (fig. 23). This observation confirms SOLEREDER'S (4) statement that "only simple perforations have been observed in the woody and herbaceous genera of this group with the single exception of *Paeonia.*" In the leaf trace of a species of *Paeonia* (figs. 24, 25) in the region of the primary wood, the perforations show the more primitive pitted condition combined more or less with the more modern scalariform condition. The protoxylem elements are visible at the left of the figures, and here again in close proximity to the primary wood (fig. 25) we have the vessel with the pitted side wall.

The Betulaceae, a group of the Angiosperms often regarded as primitive, is of importance in regard to the evolution of the angiospermous vessel as compared with the origin of the vessel in Gnetales. THOMPSON (5) concludes that the mode of origin of vessels in the two groups is quite different. Moreover, he states that "since the Gnetalean vessel usually has only two rows of circular pits, no matter how the fusions take place no scalariform bars can result." It has already been seen that in *Gnetum scandens* (figs. 12, 13) the scalariform perforations are very evidently the result of fusion of opposite circular pits. Further evidence of such progression in the evolution of the perforation is seen in the Betulaceae. The typical end wall of the vessel in this group is scalariform. Such an end wall is seen in the stem wood of *Betula alba* in radial aspect in fig. 28. In this type of scalariform end wall there is usually no indication of the derivation of the scalariform perforation from fusion of pits, although instances of this condition are not infrequent even in the mature wood. It is the vessels which lie near the primary wood which are of greatest interest from an evolutionary standpoint. Fig. 26 shows three such vessels, the spiral elements of the protoxylem lying to the left of them. The vessel nearest the protoxylem has a perforation which is intermediate between scalariform and pitted, this condition being most clearly recognizable at the middle of the figure. In the vessel next to the right the transitions appear only at the top and bottom of the perforation, while in the third vessel the fusion of pits is practically complete. Haphazard fusion is evident in the lower portion of the perforation. Fig. 27 illustrates another vessel taken from a different preparation, in which the perforation is much less extensive than in the preceding figure, and the derivation of the scalariform perforation from pit fusions at the top and bottom is particularly clear.

The same conditions which have been noted for *Betula* are found also in *Alnus*. The typical end wall of the vessel is scalariform, as seen in fig. 31. Practically no indication of pit fusions is seen, but fig. 29 is evidence that such fusion has taken place. In the lower part of the figure more or less haphazard fusion is evident, while in the upper region two elongated pits are still distinct. A higher magnification of the same end wall is seen in fig. 30. It is clear for the Betulaceae as exemplified by *Betula* and *Alnus*, as for the Magnoliaceae, that the scalariform perforation as shown by primitive regions is derived from pit fusions and does not represent the persistence of a primitive scalariform condition of the vessel wall.

Passing to a consideration of a type of vessel in the Angiosperms which is characterized by porous and not scalariform perforations, and taking a form nearly allied to the Betulaceae, *Quercus velutina*, we invariably find in the mature wood porous perforations which in the smaller vessels sometimes show a border like that characteristic of similar perforations in *Gnetum*. SOLEREDER (4) has already pointed out in the oak and other representatives of the Fagaceae that scalariform perforations are characteristic of regions near the primary wood. I have been able to confirm this general statement of SOLEREDER in regard to the oak. A radial section of *Quercus velutina* (fig. 32) through the primary wood of the leaf trace shows a very interesting condition in the perforation. The transition from the pitted to the scalariform condition is very clear. Usually the perforations of the vessels in the primitive region of *Quercus* are scalariform only, without transition from the pitted condition. In *Fagus* one frequently finds vessels with scalariform perforations even in the mature wood.

We may now consider the Rosaceae, a higher group, characterized in general by porous perforations of the vessels. Taking first a herbaceous representative of the family, fig. 33 shows a vessel in the region of the primary wood of the stem of *Potentilla monspeliensis*, an annual herb. The vessels in this region have scalariform perforations which pass gradually, by the disappearance of transverse bars, into porous perforations. SOLEREDER has described a similar condition in *Potentilla fruticosa*, and it appears to be widespread in the genus. As a woody representative of the group, *Cydonia* is interesting as showing the scalariform perforation of the vessel in the region of the primary wood (fig. 34), as found in *Potentilla*. An interesting situation is presented by the organization of the vessel in the primitive region of the leaf trace, in its course in the stem of *Cydonia japonica* (fig. 35), in which the perforation is pitted, a very significant condition. Taking the Rosaceae as illustrated by *Potentilla* and *Cydonia*, it seems clear that the porous condition of the perforation has been preceded by the scalariform, and the scalariform in turn by the pitted.

In the Vitaceae the lateral walls of the vessels in contact with other vessels are practically universally scalariform. This condition is of particular interest because the scalariform lateral sculpture of vessels is a phenomenon of rare occurrence in most angiospermous orders, being usually confined to a single genus and occasionally to a single species. If we examine the primitive region of the stem near the primary wood, vessels with pitted lateral walls may often be found (fig. 37). A further fact which has some bearing on the situation is the occurrence of pits on those walls of the vessels which are in contact with the vasicentric parenchyma, characteristic of this group. This situation is not the less striking because ray cells and even longitudinal parenchymatous elements in the Angiosperms in general are frequently related to vessels by means of fusion pits of a scalariform nature. This condition is widespread among the Angiosperms. It has been pointed out by BAILEY (1) in this connection that in modern species of *Pinus* the lateral pits of the rays often undergo fusions. Similar conditions are often found in the Podocarpineae, Taxodineae, and Cupressineae, and has even been found in Paleozoic Gymnosperms. Fig. 38, illustrating the same section as fig. 37, farther out from the primary wood, shows the type of vessel characteristic of the mature wood of the Vitaceae as a group, with scalariform sculpture. It is apparently quite clear that the vessel with scalariform lateral pits in the Vitaceae has been derived from a pitted predecessor, and that it is not a primitive vessel type in this family.

Turning now to the perforation of the vessels in the Vitaceae in the mature wood of *Leea* and *Vitis*, the vessels are characterized by large open terminal pores. This confirms SOLEREDER's statement that the vessels in the Vitaceae "have simple circular or elliptical perforations." Such a perforation is seen in the radial section of the stem of a species of *Leea* in the region of the primary wood (fig. 36) at the right of the figure. A very interesting fusion scalariform perforation is seen in the vessel on the left. The photograph in this case is not clear, owing to the thickness of the section, but seen under the microscope it is an unusually vivid demonstration of the course of events in the evolution of the open pore. Fig. 39 shows vessels from the leaf trace of *Vitis* in its course in the stem. On the left in the region of the primary wood two vessels show scalariform perforations; to the right is the single open pore typical of the vessels of the group. An interesting reversion to the primitive type of perforation in this genus is seen in the radial section at the end of the annual ring (fig. 40). The spring vessels show the open pore characteristic of the mature wood, but in the summer wood, which is in some respects a primitive region, we have the reversion to the scalariform type of perforation characteristic of the regions of the primary wood and of the leaf trace. From the evidence given it seems clear that in the Dicotyledons as in the Gnetales the scalariform perforations have arisen by the fusion of pits, and that this fusion may be haphazard or serial.

Conclusions

This investigation covers the origin of the vessel in *Pteris*, in Gnetales, and in dicotyledonous Angiosperms. In *Pteris* the primitive condition of the vessel is scalariform, with the obvious tendency to the development of pitted sculpture in the end wall of the element. It is of interest to note that in the Osmundaceae and Ophioglossaceae the pitted as contrasted with the scalariform sculpture appears in the side walls of the vascular elements.

In Gnetales the vessels have obviously been derived from pitted and not from scalariform tracheids. Their evolution is connected with the appearance of particularly large pits in the end walls of the vascular elements, which first lose their membranes and subsequently undergo fusions, either transversely or irregularly. As in *Pteris*, it is the perforation region of the vessel which shows the greatest advance and specialization. In the Dicotyledons two general types of vessels are found, those with scalariform perforations and those with porous perforations. Investigation of the first type from the Magnoliaceae and Betulaceae appears to establish the fact that the perforations have arisen by pit fusions precisely as in the higher Gnetales. In the second type the vessel with porous perforation, often with bordered margins as in *Gnetum*, in most cases in the Angiosperms has had its immediate origin from the vessel with scalariform perforations. These in turn, as illustrated by *Quercus* and *Cydonia*, have been derived from the fusion of pitted perforations. It follows that the mode of origin of the vessel in the Dicotyledons and Gnetales is essentially similar, in both cases being the consequence of the fusion of open bordered pits, either in rows or irregularly.

These remarks apply to the end wall of the vessel, particularly to the perforation. In the few cases among the Angiosperms where the lateral vascular walls are scalariform, it appears clear that the scalariform lateral pits have resulted from the horizontal fusion of circular or oval pits. It is further to be noted that the scalariform sculpture appears first in the terminal region of the vessel and may later appear in the side wall, always resulting from pit fusions. It follows that the vessel of the Angiosperms as of the Gnetales has been derived not from the scalariform but from the pitted tracheid. In this respect the vessel is in harmony with the other evolutionary developments in the wood, since according to the best established view both the mechanical fibers and the longitudinal parenchymatous elements of higher plants have been derived from the pitted tracheid (3). It would be surprising if the vessel, which is much later in geological times than longitudinal storage elements and mechanical elements of strength, should have originated from a type more primitive than the pitted tracheid.

Summary

1. In *Pteris* the scalariform perforation of the vascular end wall often becomes pitted.

2. In the *Gnetum* type of vessel the fusion of pits to form the porous perforation is haphazard, but in *Gnetum scandens* the fusion of pits is often more regular, resulting in a scalariform perforation.

3. Haphazard fusion of pits is also found in *Paeonia*, *Cydonia*, and *Leea;* while in *Liriodendron*, *Magnolia*, *Paeonia*, *Betula*, *Alnus*, *Quercus*, and *Vitis* the fusion is often serial, resulting in scalariform perforations.

4. The evolution of the perforations of the vessels in Gnetales and Dicotyledons is similar, and in both cases is the result of pit fusions.

5. From evidence derived from a consideration of primitive and conservative regions in *Liriodendron*, *Magnolia*, *Paeonia*, and *Vitis*, it may be concluded that the primitive type of vessel in the Angiosperms is pitted, and has been derived from the pitted tracheid as have the mechanical and longitudinal storage elements of the wood.

This investigation has been carried on in the laboratories of plant morphology at Harvard University under the direction of Dr. E. C. JEFFREY. In conclusion I wish to express my thanks to him for the material supplied and for his invaluable aid throughout the work.

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EXPLANATION OF PLATES XVI–XX

PLATE XVI

FIG. 1.—Longitudinal radial section of bundle of rhizome of *Pteris aquilina;* ×250.

FIG. 2.—End wall of vessel of *Pteris aquilina* in face view, reticulated type; ×250.

FIG. 3.—End wall of vessel of *Pteris aquilina* in face view, scalariform type; ×250.

FIG. 4.—Portion of vessel of *Pteris aquilina*, profile view; ×166.

FIG. 5.—Longitudinal radial section of young twig of *Ephedra;* ×125.

FIG. 6.—Longitudinal radial section of older twig of *Ephedra;* ×250.

FIG. 7.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×62.

FIG. 8.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×187.

PLATE XVII

FIG. 9.—Longitudinal radial section of stem of *Gnetum Gnemon* type; ×250.

FIG. 10.—Longitudinal radial section of stem of *Gnetum scandens* in region of primary wood; ×250.

FIG. 11.—Longitudinal radial section of leaf trace of *Gnetum scandens;* ×40.

FIG. 12.—Longitudinal radial section of leaf trace of *Gnetum scandens* showing end wall; ×250.

FIG. 13.—Longitudinal radial section of leaf trace of *Gnetum scandens;* ×125.

FIG. 14.—Longitudinal radial section of mature wood of *Welwitschia mirabilis;* ×250.

FIG. 15.—Longitudinal radial section of leaf trace of *Welwitschia mirabilis;* ×250.

FIG. 16.—Longitudinal radial section of mature secondary wood of small twig of *Liriodendron Tulipifera;* ×250.

PLATE XVIII

FIG. 17.—Longitudinal radial section of root of *Liriodendron Tulipifera* in region of primary wood; ×187.

FIGS. 18–20.—Longitudinal radial section of root of *Liriodendron Tulipifera* in region of primary wood; ×250.

FIG. 21.—Longitudinal radial section of root of *Magnolia Frazeri* in region of primary wood; ×250.

FIG. 22.—Longitudinal radial section of first annual ring in stem of *Magnolia Frazeri;* ×250.

FIG. 23.—Longitudinal radial section of stem of *Paeonia moutan;* ×125.

FIG. 24.—Longitudinal radial section of leaf trace of species of *Paeonia;* ×250.

PLATE XIX

FIG. 25.—Longitudinal radial section of leaf trace in species of *Paeonia;* ×250.

FIG. 26.—Longitudinal radial section of stem of *Betula alba* in region of primary wood; ×250.

FIG. 27.—Longitudinal radial section of vessel of *Betula alba* in region of primary wood; ×375.

FIG. 28.—Longitudinal radial section of secondary wood of *Betula alba;* ×250.

FIG. 29.—Longitudinal radial section of stem of *Alnus incana* in region of primary wood; ×250.

FIG. 30.—Same as fig. 29; ×375.

FIG. 31.—Longitudinal radial section of secondary wood of *Alnus incana;* ×375.

FIG. 32.—Longitudinal radial section of leaf trace of *Quercus velutina* in region of primary wood; ×375.

PLATE XX

FIG. 33.—Longitudinal radial section of stem of *Potentilla monspeliensis* in region of primary wood; ×250.

FIG. 34.—Longitudinal radial section of stem of *Cydonia vulgaris* in region of primary wood; ×250.

FIG. 35.—Longitudinal radial section of leaf trace of *Cydonia japonica;* ×250.

FIG. 36.—Longitudinal radial section of stem of species of *Leea* in region of primary wood; ×250.

FIG. 37.—Longitudinal radial section of stem of species of *Vitis* in region of primary wood; ×250.

FIG. 38.—Same as fig. 37, farther out from primary wood; ×250.

FIG. 39.—Longitudinal radial section of leaf trace of species of *Vitis;* ×250.

FIG. 40.—Longitudinal radial section of spring and summer wood in species of *Vitis;* ×250.